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Abundance, horizontal and vertical distribution of fish in eastern Weddell Sea micronekton

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Summary. The spatial distribution and species composition of high-Antarctic ichthyonekton was investigated during the EPOS 3 cruise by *RV Polarstern* in the eastern Weddell Sea during January–February 1989. A multiple rectangular midwater trawl was used to collect samples from the surface to near the sea floor at 11 stations along a 245 km transect off Halley Bay. Early larval stages of 18 species, representing about 24% of the known Weddell Sea ichthyofauna, were present in the water column. The Antarctic silver-fish, *Pleuragramma antarcticum*, overwhelmingly dominated the catches comprising 84.5% of the 5022 specimens caught. The abundance of this species markedly increased towards the offshore end of the transect with the highest numbers occurring near the shelf-break front associated with the westerly current of the southern limb of the Weddell Gyre. The increased abundance of *P. antarcticum* in continental slope waters was attributed to deflection of the East Weddell Coastal Current beyond the shelf/slope break by fringing ice shelves. Most larval and juvenile fish were found in the seasonally warmed upper 0–70 m layer of the Antarctic Surface Water where conditions occurred that appeared to be favourable to both feeding and growth. Cluster analysis indicated that inner-, central- and outer-shelf assemblages were represented and that the species composition was most effectively described by reference to water mass and depth.

Introduction

The high Antarctic marine ecosystem is one of the least well known in the World Ocean. During the third leg of the European Polarstern Study (EPOS 3), from *RV Polarstern* 13 Jan 1989 to 10 March 1989, it was planned to extend knowledge about the high Antarctic ecosystem by means of an integrated study of the benthic and pelagic communities in relation to biotic and abiotic environmental conditions. One of the main objectives was to describe the micronekton distributions, compare these with previous observations and identify the principal biological and physical factors associated with these patterns (Arntz and Hureau 1990). Sampling was planned to be undertaken within a 'box' in the coastal polynya adjacent to Halley Bay. The unusual absence of pack-ice in the eastern Weddell Sea during summer 1989 enabled the 'box' to be extended to a 'transect' from the ice-shelf near Halley Bay across the continental shelf to the continental slope. An additional transect and time station were performed near and Kapp Norwegia (Fig. 1).

The ichthyonekton of the high Antarctic is not well known and there have been few accounts of the early life history stages of fish in the Weddell Sea. Descriptions of the occurrence and distribution of ichthyoplankton in the region can be found in Hempel et al. (1983), Kellermann (1986), Ekau et al. (1987), Piatkowski (1987), Boysen-Ennen and Piatkowski (1988), Hubold (1990), Hubold and Ekau (1990) and Piatkowski et al. (1990). The dominant species is *Pleuragramma antarcticum* and the biology of this species has been reviewed by Hubold (1985; 1991). The major characteristics of the larval stages of Antarctic fish species assemblages, including those from the Weddell Sea, have been reviewed by Loeb et al. (In Press). Current knowledge about the ecology of fish inhabiting the Weddell Sea has been presented in the authorative review by Hubold (1992).

The eastern continental shelf of the Weddell Sea basin is very narrow and mostly covered by shelf-ice, whereas the southern shelf is broad, extending 200–400 km offshore. The hydrography within this basin is dominated by the wind-driven clockwise circulation of the Weddell Gyre (Fig. 1). The gyral circulation involves the whole water column and conforms to bottom topography. Inflow of water occurs as a well defined current (East Wind Drift) flowing west along the slope to the vicinity of Halley Bay where it divides into continental slope and coastline branches (Gordon et al. 1988). The coastline branch is directed southward into the Filchner Trench while the slope branch flows around the Weddell Sea basin before

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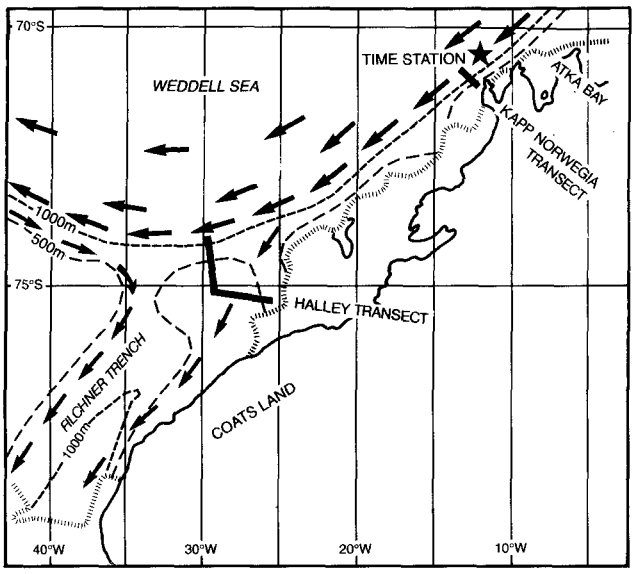

Fig. 1. Eastern Weddell Sea: bathymetry, circulation patterns and EPOS3 sampling localities. Arrows denote surface currents, hatched line indicates coast formed by ice shelf

exiting northward into the open ocean where it merges with the Antarctic Circumpolar Current at the Weddell-Scotia Confluence.

Very low seawater temperatures (-1.8°C) prevail over the shelf and Antarctic Bottom Water (ABW) is produced in association with the major ice-shelves in the southern Weddell Sea (Gill 1973; Rohardt et al. 1990; Fahrbach et al. 1992 a). In summer a warmed (>0°C) surface layer is usually formed in the upper 50–100 m (Deacon 1964; Rohardt et al. 1990).

Ice dominates the marine environment in the Weddell Sea. The coast is almost entirely fringed by continental ice shelves and glaciers thereby greatly restricting shallow water habitats. Permanent sea-ice persists in the western part of the Gyre and in winter seasonal sea-ice covers the entire area except for small zones where offshore winds or upwelling permit development of polynyas. Primary production in the Southern Ocean is strongly influenced by seasonal light and ice cycles resulting in a short bloom which may be locally reduced and inconsistent due to shading by sea-ice (White 1973). Weddell Sea primary production is of the order of 20–50 $g C m^{-2} y^{-1}$ (von Bodungen et al. 1988)

During EPOS 3 the typical thermal stratification due to surface warming was enhanced by an extended period of calm weather and unusual lack of surface ice. The Antarctic Surface Water (ASW) was characterised by steep temperature gradients with temperatures about $+1$°C at the surface, usually decreasing to -1.8°C by 100 m depth and to as low as -2°C over the inner trench (Fig. 2 and 3). Disruption of the horizontal thermal stratification was evident at the inner trench and in the vicinity of the continental shelf/slope break. Doming of the isotherms over the inner trench indicated very cold, low

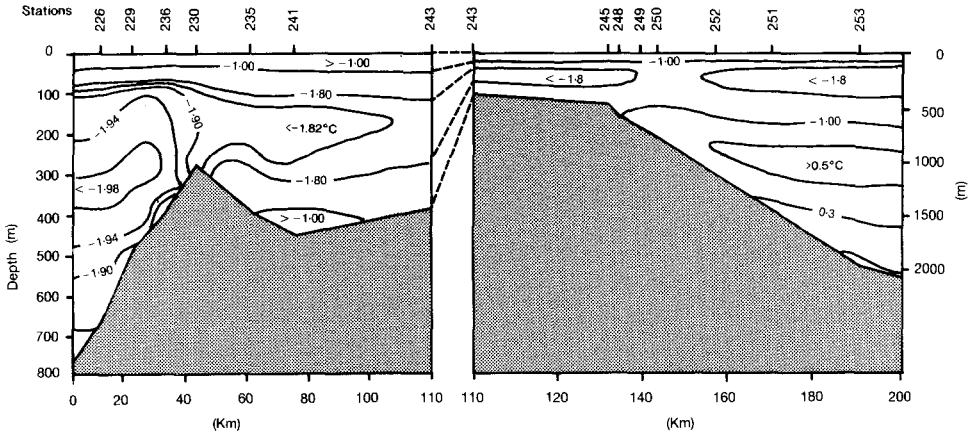

Fig. 2. Halley Transect: seawater temperature profile (redrawn after Rohardt et al. 1990)

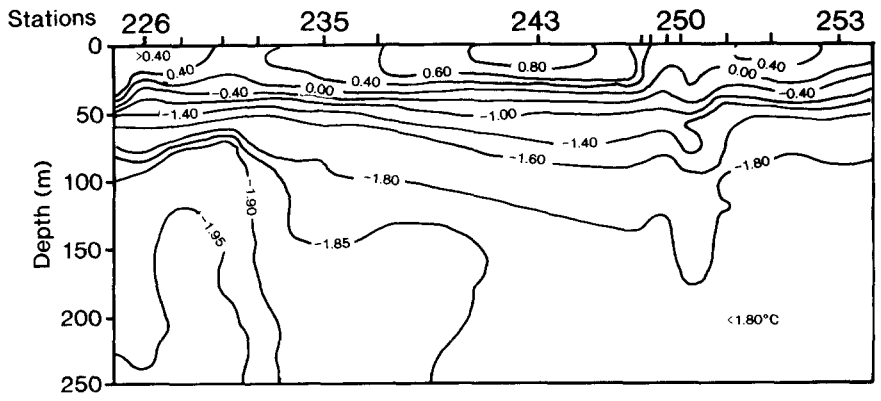

Fig. 3. Halley Transect: detail of isotherms in the top 250 m

salinity water approaching the surface; the position of the shelf-break front was indicated by marked undulation of the isotherms between stations 249 and 250 (Fig. 3). The shelf/slope junction and inner trench were both associated with strong horizontal currents (cf Rohardt et al. 1990, Figs. 19–21). An unusual feature of the vertical temperature structure along the Halley Transect was a warm 'pool' over a seabed basin at station 241 (Fig. 2). This lens of water was thought to be a residual from encroachment by Warm Deep Water over the continental shelf (Fahrbach et al. 1992 b).

Ice cover usually greatly restricts marine research work over the Antarctic Continental Shelf and ice-fields often persist in the Weddell Sea throughout the year. Thus ichthyological sampling in the region has been intermittent and mostly undertaken during summer months (December-February). Some sampling has been carried out during spring (October–November; Hubold 1990). Most ichthyonekton samples have been collected over or near the shelf in the coastal polynya of the eastern and southeastern Weddell Sea off Vestkapp (Hubold 1990) and Halley Bay (Piatkowski et al. 1990). The ichthyofaunal species composition is relatively diverse with more than 75 species from 43 genera and 14 families recorded (Hureau et al. 1990). The larval stages of 38 (51%) of these have been identified (Table 1). The species composition of adult assemblages is similar to that recorded at other continental embayments such as Prydz Bay (Williams, pers. comm.) and the Ross Sea (Iwami and Abe 1981). Within the Weddell Sea progressively larger proportions of

Table 1. Fish species identified from the Weddell Sea ichthyonekton

Family (Σ spp)	Species	Source
Nototheniidae (10)	*Pleuragramma antarcticum*	1 2 3 4 5 6 7 8 9 10
	Trematomus lepidorhinus	6 7 8 9 10
	Trematomus centronotus	6 8
	Trematomus scotti	2 6 8 10
	Trematomus eulepidotus	2 3 6 7 8
	Pagothenia hansoni	7
	Pagothenia brachysoma	6 8
	Aethotaxis mitopteryx	1 5 6 7 8 9 10
	Notothenia kempi	3
	Nototheniops larseni	2
Channichthyidae (9)	*Chionodraco myersi*	6 7 8 9 10
	Chionodraco hamatus	9 10
	Chionodraco rastrospinosus	2 9 10
	Pagetopsis maculatus	2 4 6 7 8 10
	Pagetopsis macropterus	6 7 8
	Dacodraco hunteri	1 4 6 7 8 9 10
	Chaenodraco wilsoni	6 7 8 9 10
	Cryodraco antarcticus	6 7 8 9 10
	Chionobathyscus dewitti	8
Bathydraconidae (8)	*Racovitzia glacialis*	3 6 7 8 9 10
	Prionodraco evansii	1 3 6 8 9 10
	Akarotaxis nudiceps	8 9 10
	Gerlachea australis	6 7 8 9 10
	Bathydraco antarcticus	8 9 10
	Bathydraco sp.	9 10
	Gymnodraco acuticeps	6 8
	Parachaenichthys charcoti	3
Artedidraconidae (2)	Artedidraconid sp A	9 10
	Artedidraconid sp B	9 10
Bathylagidae (1)	*Bathylagus antarcticus*	1 3 4 5 10
Paralepididae (1)	*Notolepis coatsi*	1 3 5 9 10
Myctophidae (3)	*Electrona antarctica*	3 9 10
	Gymnoscopelus braueri	9 10
	Gymnoscopelus opisthopterus	9 10
Liparididae (1)	Liparid sp.	4
Zoarcidae (1)	Zoarcid sp.	4
Macrouridae (1)	*Macrourus holotrachys*?	4 6
Muraenolepididae (1)	*Muraenolepis microps*	6

(Sources: 1 Boysen-Ennen and Piatkowski 1988; 2 Kellermann 1986; 3 Hempel et al. 1983; 4 Ekau et al. 1987; 5 Piatkowski 1987; 6 Hubold 1990; 7 Hubold and Ekau 1990; 8 Kellermann 1990; 9 Piatkowski et al. 1990; 10 This study)

pelagic species are represented with increasing latitute (Hubold 1991) although the species diversity remains relatively constant (Schwarzbach 1988). Nototheniids, channichthyids and bathydraconids dominate the shelf assemblages; myctophids, bathylagids and paralepidids comprise the oceanic component beyond the shelf-break front. Artedidraconids, liparids and zoarcids are common components of the demersal fauna but their larval stages are rarely encountered. Larval *P. antarcticum* typically dominate the shelf ichthyonekton after hatching in November/December (Hubold 1985; 1990) and may comprise more than 90% of the larvae captured during summer months (Hubold 1990; Piatkowski et al. 1990).

Ichthyonekton from the Antarctic Peninsula and South Georgia region exhibit distinct seasonal changes in abundance and species composition (Burchett et al. 1983; Kellermann 1989; North and White 1987) and, although there are few winter data, the Weddell Sea ichthyonekton also appear to exhibit a seasonal succession of dominant species. Hubold (1990) reports a sequence of *Aethotaxis mitopteryx-Pleuragramma antarcticum-Trematomus scotti-Trematomus lepidorhinus-Trematomus eulepidotus* for spring through summer in the eastern Weddell Sea. The early occurrence of *P. antarcticum* and A. *mitopteryx* larvae coincides with a rapid increase in the abundance of larval and post-larval calanoid copepods which are important prey items (Hubold and Ekau 1990). The distribution and temporal occurrence of piscivorous channichthyid larvae (eg., *Chionodraco myersi*, *Pagetopsis* spp., and *Dacodraco hunteri*) are closely associated with the occurrence of abundant notothenid prey species such as *P. antarcticum* (Hubold 1990; Hubold and Ekau 1990).

The horizontal and vertical distribution patterns of most species are not well known. However, it is evident that the continental slope current has a marked influence by advecting the pelagic stages around the Weddell Sea basin. Advention by the East Wind Drift and retention zones in the southern Weddell Sea have been implicated in influencing the life histories of several species and described for *P. antarcticum* Hubold (1985). Vertical ontogenetic separation in *P. antarcticum* was described by Hubold (1985) and shown in the preliminary results in this study (Hureau et al. 1990). Application of a depth/distance index to the eastern shelf ichthyonekton demonstrates a general separation of neritic and oceanic assemblages (Hubold 1990) which is less well defined than that observed at lower latitudes.

Preliminary micronekton results from the EPOS 3 cruise have been given by us in Piatkowski et al. (1990). We here describe the detailed results of ichthyonekton from RMT8 samples collected along the Halley transect.

Materials and methods

A multiple rectangular midwater trawl (RMT8+1M) was used to collect micronekton at 11 sampling sites (28 Jan 1989 – 10 Feb 1989) along a 200 km segment of the 245 km transect (Fig. 4). The RMT8+1M comprised three 1 m^2 nets (RMT1, 335 µm mesh) and three 8 m^2 nets (RMT8, 4.5 mm mesh). Each pair of RMT1 and RMT8 net was opened and closed by electronic command from the

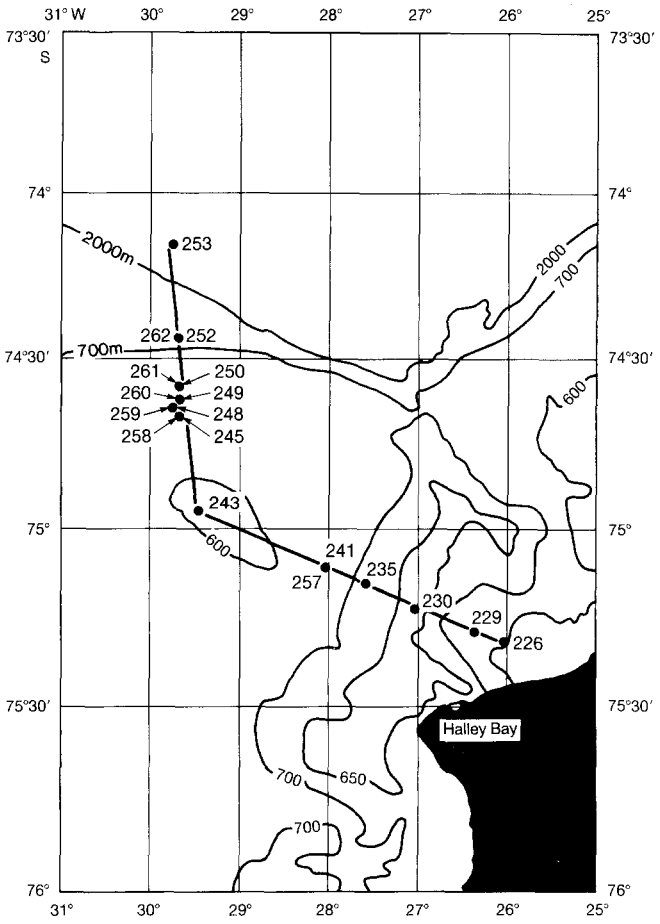

Fig. 4. Halley transect: station location and bathymetry

vessel. Data from the nets and commands were transmitted to a ship-board computing system via an 18 mm conducting trawl wire. Depth, distance travelled, tilt angle, status of the net and water temperature were displayed and recorded in real time using software developed by the Alfred-Wegener-Institute for Polar Research (Dimmler and Klindt 1990). Summary information about each RMT net deployment is given in the station data annex of the EPOS 3 cruise report (Arntz et al. 1990). The stations were classified in relation to the bathymetry and the prevailing hydrography as follows:

'inner-shelf' stations (226, 229, 230),
'central-shelf' stations (235, 241, 245, 248, 249; 257, 258, 259, 260),
'outer-shelf' stations (250, 252, 253; 261, 262).

The shelf-break front was located between stations 249 and 250.

In addition, micronekton samples were collected using the RMT8+1M at Kapp Norwegia (15–21 Feb 1989) and at a 24 h Time Station (23/24 Feb 1989) over the continental slope near to Kapp Norwegia (Fig. 1). Only small numbers of fish were caught at these stations but these data are reported here to complete the ichthyonekton composition results for EPOS 3.

The objective was to sample the water column from the surface to near the seafloor at each station. Oceanographic studies (Rohardt et al. 1990; Rabitti et al. 1990) indicated a well stratified upper water column with the warmed surface layer extending to ca 70 m and the temperature minimum at about 200 m. The 0–300 m layer was sampled at 0–70 m, 70–200 m and 200–300 depth strata to take account of the vertical thermal structure. Water depths were greatest at the north-western end of the transect and so six of the seven outer stations (stations 241–252) were sampled at depths between 300 m

and near bottom (stations 257–262) (cf Figs. 4 and 6). It is important for the reader to note that this results in there being two stations (one = <300 m and another = >300 m) at each of the outer sampling sites. Sampling below 300 m at the 'inner' stations was not possible owing to time limitations.

The net deployment was standardised using an upward oblique haul; the descent rate was 0.4 m s^{-1} and ascent rate 0.3 m s^{-1}. Total ichthyonekton abundance values estimated from net caught samples can be confounded by marked diurnal variation in vertical distribution and net avoidance, resulting in maximum abundances occurring in samples collected at night. RMT net sampling during EPOS 3 was consistently undertaken during the early morning. Therefore the abundance values should be consistent within the data set but are likely to be substantial under-estimates.

The net contents were usually processed within 2 h after capture. Samples from each net were maintained in seawater at ambient surface temperature before treatment in the laboratory to avoid undue specimen contraction. Initial processing included wet volume measurement and identification of the dominant components. RMT1 samples were fixed without further treatment and processed ashore. Fish and squid were sorted from the RMT8 samples; the remaining components were fixed for later analysis. Fish from the RMT8 samples are the basis for this account.

Each fish specimen was identified, measured and any distinctive features recorded before being fixed and stored in buffered 4% formaldehyde solution. Abundance values were standardised as numbers per filtered volume (n/1000 m^3) calculated from distance travelled and net aperture corrected for tilt angle.

The diet of the larval fish was determined by examination of the stomach contents from a small number of samples. This was done for comparison with observations by Hubold and Ekau (1989) and to identify the species of fish consumed by larval channichthyids.

Community and cluster analyses using Bray-Curtis index of similarity were carried out using the software package COMM developed at the Institut für Polarökologie, Kiel (Piepenburg and Piatkowski in press). Other statistical calculations were carried out using the MINITAB package version 7.1 (Pennsylvania State Univ.)

Results

Abundance

A total of 5022 ichthyonekton specimens were collected along the Halley transect (Table 2). Notothenioids were the most commonly occurring group comprising 97.7% of the individuals; postlarval *Pleuragramma antarcticum* were the overwhelmingly dominant component comprising 84.5% of the total catch. *P. antarcticum* was the dominant species at most stations except those over the inner-shelf (stations 226, 229 and 230) where *Aethotaxis mitopteryx* was more or equally abundant (Table 3). Abundance values, standardised for volume swept, indicated that the ichthyonekton were least abundant at inner-shelf stations and most abundant at the outer end of the transect beyond the shelf-break front (Table 3). Only 175 fish were collected from RMT8 samples at Kapp Norwegia and the 24 h Time Station (Table 4).

Species composition

A total of 18 species were collected along the Halley transect (Table 2). Among the standard 0–300 m hauls the inner-shelf stations (226–230) showed least diversity with three or four species occurring at each station: seven to

Table 2. Halley transect: ichthyonekton species occurrence, abundance, and size (mm)

Species	Number	%	Mean	Size (mm) ±sd	Range
Pleuragramma antarcticum	4242	84.5	16.1	1.8	10–22
Chionodraco myersi	282	5.6	28.8	3.8	19–46
Pagetopsis maculatus	212	4.2	17.9	1.6	14–22
Aethotaxis mitopteryx	76	1.5	21.3	2.8	13–30
Bathylagus antarcticus	57	1.1	29.5	12.9	9–50
Notolepis coatsi	30	0.6	37.2	12.7	5–62
Racovitzia glacialis	30	0.6	19.4	2.6	13–24
Electrona antarctica	28	0.6	26.6	8.7	5–39
Prionodraco evansii	21	0.4	23.9	2.6	16–29
Dacodraco hunteri	18	0.4	20.0	2.9	16–26
Trematomus lepidorhinus	11	0.2	19.0	2.3	15–22
Akarotaxis nudiceps	4	<0.1	22.5	0.7	22–23
Bathydraco antarcticus	4	<0.1	25.0	1.4	24–26
Artedidraco sp A	2	<0.1	16.0	1.0	15–17
Gymnoscopelus opisthopterus	2	<0.1	30.8	4.7	25–41
Chaenodraco wilsoni	1	<0.1	21.0	–	–
Cryodraco antarcticus	1	<0.1	25.0	–	–
Gerlachea australis	1	<0.1	45.0	–	–
Total	5022				
Notothenioidei	4905	97.7			
Nototheniidae	4329	86.2			
Channichthyidae	514	10.2			
Bathydraconidae	60	1.2			
Artedidraconidae	2	<0.1			
Others	117	2.3			

Table 3. Halley transect: ichthyonekton abundance from RMT8 samples (n/1000 m^3) Stations 226–253: 0–300 m (net 1 = 0–70 m, 2 = 70–200 m, 3 = 200–300 m), Stations 257–262: > 300 m

Station	226			229			230			235			241			245			248			249		
Species/Net	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
P. antarcticum	0.2	0.5	1.0	0.3	–	0.5	–	–	0.5	3.0	2.0	0.2	1.0	4.0	11.0	0.6	2.0	11.0	3.0	0.5	36.0	8.0	5.0	48.0
C. myersi	–	–	–	–	–	–	–	–	–	–	0.2	4.0	0.2	–	1.0	0.6	0.1	5.0	–	0.2	1.0	0.2	–	1.0
P. maculatus	–	–	–	–	–	–	–	–	0.2	0.4	0.5	1.0	–	1.0	3.0	0.4	0.3	2.0	–	–	1.0	–	–	1.0
A. mitopteryx	–	0.4	3.0	–	–	0.8	0.3	1.0	36.0	0.3	–	0.5	–	–	0.3	–	–	–	–	–	–	–	–	–
R. glacialis	–	–	–	–	–	–	–	–	–	0.3	0.5	–	0.4	0.3	–	–	–	–	–	–	–	–	–	0.2
D. hunteri	0.8	0.4	–	0.3	–	0.3	–	0.2	–	–	–	–	–	–	–	–	–	–	–	0.3	–	–	–	–
P. evansii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.3	–	–	1.0	–	0.2	–	–	–	0.7
T. lepidorhinus	–	–	–	–	–	–	–	–	–	–	–	0.2	–	–	0.3	–	–	0.2	–	–	0.6	–	–	0.2
A. nudiceps	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	–	–	–	–	–	–
G. australis	–	–	–	–	–	–	–	–	–	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–	0.2
Bathydraco ant.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Artedidraco sp.	–	–	–	–	–	–	–	–	–	–	–	0.2	–	–	–	–	–	–	–	0.2	–	–	–	–
N. coatsi	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	0.4	0.2
Bathylagus ant.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	0.3	–	–
E. antarctica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
G. opisthopterus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
C. wilsoni	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
C. antarcticus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total (net)	1.0	1.3	4.0	0.6	–	1.6	0.3	1.2	36.7	4.0	3.2	6.3	1.6	5.3	15.9	2.0	2.8	19.4	3.0	1.4	38.9	8.7	5.4	51.5
Total (station)*		3.5			2.2			38.2			13.5			22.8 (28.5)			24.2 (26.5)			42.3 (60.4)			65.6 (87.4)	
Total species (net)	2	3	2	2	0	3	1	2	3	4	4	7	3	3	6	4	5	6	1	5	5	4	2	8
Total species (station)*		3			3			4			8			7 (10)			8 (10)			7 (7)			9 (11)	

Table 3. (continued)

Station	250			252			253			257	258	259			260			261			262		
Species/Net	1	2	3	1	2	3	1	2	3	1	1	1	2	3	1	2	3	1	2	3	1	2	3
P. antarcticum	2.0	4.0	10.0	41.0	120.0	17.0	209.0	41.0	43.0	2.0	1.1	3.4	2.4	8.3	2.3	7.3	1.6	4.0	1.0	2.9	1.7	9.8	4.9
C. myersi	–	0.1	2.0	0.8	3.0	15.0	4.0	0.7	18.0	1.4	0.2	0.4	1.1	0.6	0.5	–	–	0.3	0.2	0.1	0.4	1.0	0.8
P. maculatus	0.2	0.2	0.8	0.8	1.0	4.0	2.0	0.4	–	1.0	0.4	0.4	0.5	1.0	–	1.0	–	0.3	0.2	0.2	0.1	0.2	0.5
A. mitopteryx	–	–	–	–	–	–	–	12.0	–	0.8	–	–	–	–	1.4	5.2	0.6	0.1	0.3	0.3	–	–	–
R. glacialis	0.2	0.3	–	0.2	0.3	–	0.3	–	–	–	–	–	–	–	–	1.0	–	–	–	–	0.1	–	–
D. hunteri		0.1	0.3	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–	–	–	–	0.1	0.2	0.2
P. evansii	0.2	0.1	–	–	–	0.3	–	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–
T. lepidorhinus	–	–	–	–	–	–	–	–	–	0.1	0.2	–	–	–	–	–	–	–	–	–	–	–	–
A. nudiceps	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		–	–
G. australis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bathydraco ant.	–	–	–	0.1	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Artedidraco sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
N. coatsi	0.4	0.4	–	–	–	–	–	–	–	–	0.2	–	–	–	0.2	–	0.1	0.4	0.5	0.2	0.3	0.2	–
Bathylagus ant.	0.2	0.1	–	–	–	–	–	–	–	–	0.2	–	–	–	0.5	–	–	–	0.1	–	0.2	–	5.1
E. antarctica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–	0.3	1.0	1.9
G. opisthopterus	–	–	–	–		–	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	0.2
C. wilsoni		–	–	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–
C. antarcticus	–	–	–	–	–	–	–	–	–	0.1	–	–		–	–	–	–	–	–	–	–	–	–
Total (net)	3.2	5.3	13.1	42.9	124.5	36.3	215.3	54.1	61.3	5.7	2.3	4.2	4.0	9.9	4.9	14.5	2.4	5.1	2.1	3.7	3.2	12.4	13.6
Total (station)*		21.3 (32.1)			203.7 (232.9)			330.7		5.7	2.3		18.1			21.8			10.8			29.2	
Total species (net)	6	8	4	5	5	4	4	4	3	9	6	3	3	3	5	4	4	5	6	5	8	6	7
Total species (station)*			7 (8)		6 (11)			6		9	6		3			8			6			9	

*Value in parenthesis, sum of samples from 0–300 m and 300 – near-seafloor

Table 4. Kapp Norwegia and Time Station: ichthyonekton species occurrence and abundance. (Species marked* were not recorded on Halley Transect)

Species	Number	%
Notolepis coatsi	56	32.0
Electrona antarctica	44	25.1
Bathylagus antarcticus	21	12.0
Pleuragramma antarcticum	18	10.3
Dacodraco hunteri	12	6.9
Chionodraco myersi	5	2.7
Chaenodraco wilsoni	4	2.3
Prionodraco evansii	2	1.1
Gymnoscopelus opisthopterus	2	1.1
*Gymnoscopelus braueri**	2	1.1
*Chionodraco hamatus**	1	0.6
*Chionodraco rastrospinosus**	1	0.6
Racovitzia glacialis	1	0.6
Trematomus lepidorhinus	1	0.6
*Trematomus scotti**	1	0.6
Bathydraco antarcticus	1	0.6
Bathydraco sp.*	1	0.6
Artedidraco sp A	1	0.6
Artedidraco sp B*	1	0.6
Total	175	

nine species were collected at the central-shelf stations (235–249) (Table 3) A slight reduction in diversity occurred at the north-west end of the transect (250–253) where six species were collected in the 0–300 m layer. If the whole water column is taken into account by including the data from the >300 m depth samples (stations 257–262) then the species richness was highest towards the outer end of the transect (Table 3).

An additional six species were collected from RMT8 samples at Kapp Norwegia and the 24 h Time Station (Table 4) resulting in a total of 24 species represented by young pelagic stages. This accounts for 32% of the known resident ichthyofauna.

Horizontal distribution

Pleuragramma antarcticum, *Chionodraco myersi* and *Pagetopsis maculatus* were the most widely distributed species. *P. antarcticum* occurred along the whole transect; fewest were caught at the inshore stations and most at the offshore stations (Fig. 5A). *C. myersi* and *P. maculatus* were rarely caught at stations near the ice-shelf (Fig. 5B).

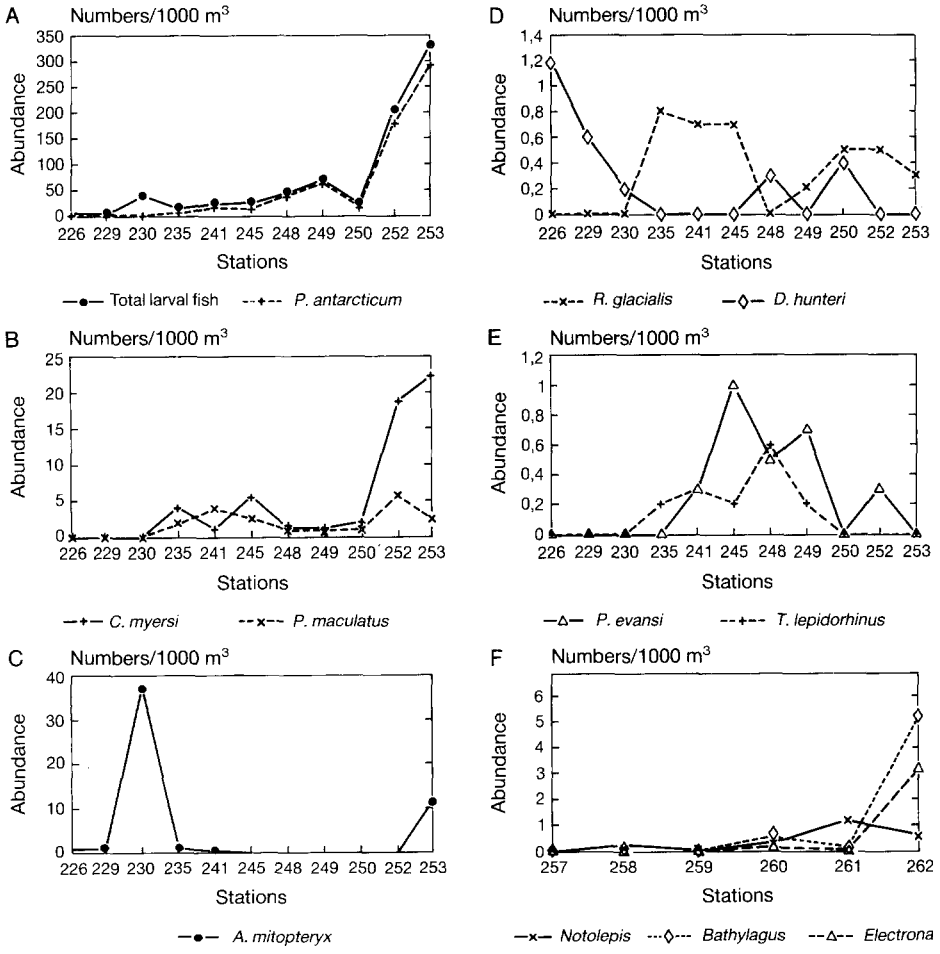

Fig. 5A–F. Halley transect: ichthyonekton horizontal distribution from RMT8 samples

Prionodraco evansii, *Trematomus lepidorhinus* and *Racovitzia glacialis* were most abundant over the central-shelf (Fig. 5D, E). *Aethotaxis mitopteryx* showed two peaks in abundance; it was the dominant species at the inner-shelf stations and also occurred at the outer end of the transect (Fig. 5C). Mesopelagic species were mainly confined to the deep samples (>300 m) collected at the outer end of the transect (Fig. 5F).

Cluster analysis to compare species composition in the 0–300 m samples from 11 transect stations indicated three assemblages. These comprised an inner-, central- and outer-shelf assemblage. Cluster analysis including data from >300 m depths indicated that the composition in the deeper water samples was most similar to that in the 0–300 m central-shelf samples. (Fig. 6). Clustering species co-occurrence in all samples indicated three species groups (Fig. 7). The mesopelagic species *Bathylagus antarcticus*, *Electrona antarctica*, *Gymnoscopelus opisthopterus* and *Notolepis coatsi* and the channichthyid *Dacodraco hunteri* formed one cluster. *P. antarcticum* was most closely associated with, and formed a second cluster with, *C. myersi*, *P. maculatus*, *Racovitzia glacialis* and *Aethotaxis mitopteryx*. The remaining notothenioid species (*Gerlachea australis*, *Prionodraco evansii*, *Trematomus lepidorhinus*, *Akarotaxis nudiceps*, and *Artedidraco* sp. A) comprised a third cluster (Fig. 7).

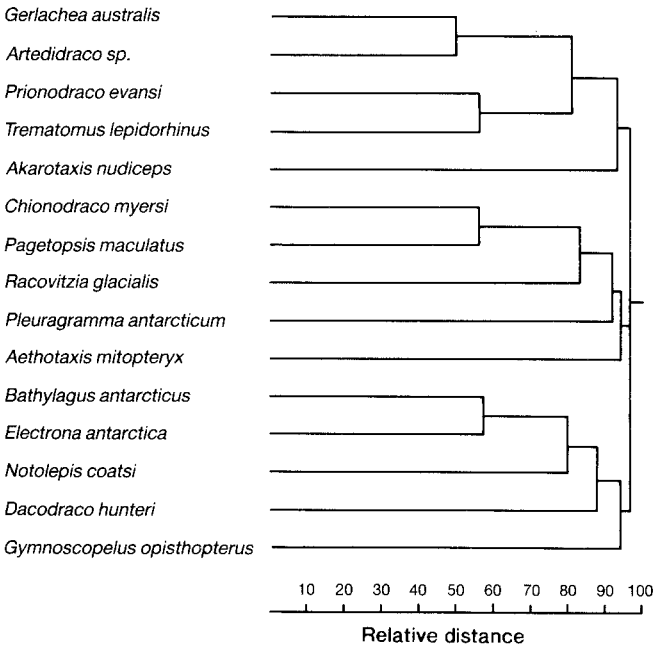

Fig. 7. Halley transect: Bray-Curtis cluster analysis dendrogram based on species co-occurrence

Vertical distribution

Most of the notothenioid species (*P. antarcticum*, *C. myersi*, *P. maculatus*, *P. evansii*, *T. lepidorhinus*, *A. nudiceps*, *G. australis*) were most abundant and occurred most frequently in the shallow 0–70 m layer (Fig. 8A–F, I). *Racovitzia glacialis* was most common above 300 m but was only caught at 0–70 m near the shelf-break front (Fig. 8G). *Aethotaxis mitopteryx* was found throughout the water column over the inner-shelf, below 300 m over the outer-shelf and at 70–200 m beyond the shelf (Fig. 8D).

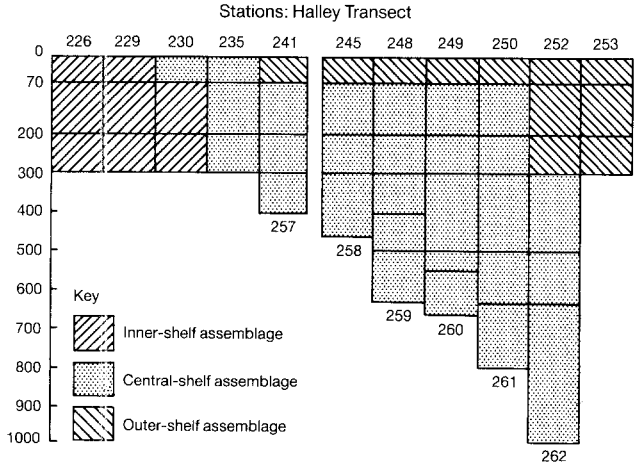

Fig. 6. Similarity of species composition from depth stratified samples based on Bray-Curtis cluster analyses of species occurrence and abundance in RMT8 nets along Halley transect

Dominant species *P. antarcticum*, *C. myersi* and *P. maculatus* (Fig. 8A–C) were found throughout the water column but were most abundant in the upper 300 m. Within the 0–300 m layer most *P. antarcticum* occurred in the 0–70 m layer except beyond the shelf-break front where most occurred at 70–200 m. *Dacodraco hunteri* was found in low numbers at a variety of depths throughout the water column (Fig. 8H) and showed no obvious distribution pattern.

Among the mesopelagic fish, the bathylagids, myctophids and paralepidids were most common in samples from the offshore and deeper stations. The myctophids, *Electrona antarctica* and *Gymnoscopelus opisthopterus* only occurred below 300 m (Fig. 8I, L) while the paralepidid *Notolepis coatsi* occurred at these and shallower depths in the vicinity of the shelf-break front (Fig. 8J). *Bathylagus antarcticus* was found over a wide depth range but was most abundant below 300 m (Fig. 8K).

The remaining species did not occur sufficiently frequently to allow their vertical distribution pattern to be fully described (Fig. 8I).

Hubold (1985) described an ontogenetic vertical separation of *P. antarcticum* age classes with progressively older classes occurring at deeper levels. Most of the *P. antarcticum* collected using RMT8 nets along the Halley Transect were '0' group fish. Only seven 'I' group fish and six 'II' group fish (after classification of Hubold and Tomo 1989) occurred along the transect; most of these were caught over the mid-shelf rise (stations 235 and 241). Analysis of the size frequency distributions of the '0' group fish demonstrated vertical stratification by size with a progressive increase in mean length with depth (Table 5). The smallest larval stages (mean 15.3 mm, SD ± 1.55) were found at the shallowest levels while the larger larvae occurred at deeper

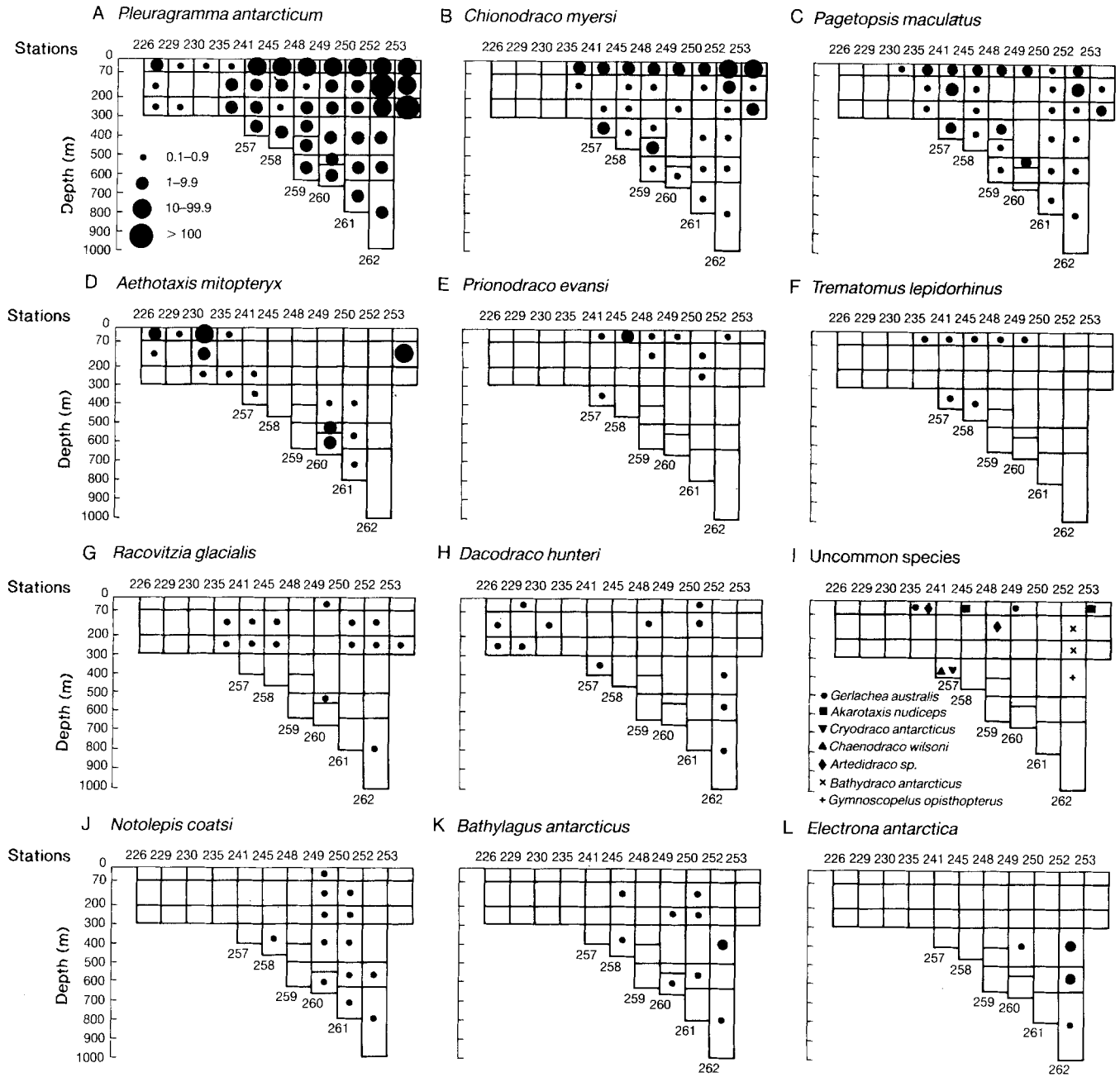

Fig. 8A–h. Halley transect: vertical distribution of species abundance (individuals/1000 m^3) for dominant species

levels with the largest in the 500–700 m layer (mean 18.2 mm, SD ± 1.27). Comparison of size frequence distributions with depth using one-way analysis of variance demonstrated that although the mean size range among the '0' group *P. antarcticum* was small the mean size occurring in different depth strata increased with depth ($p < 0.0001$).

The size frequency distribution of the other abundant species did not demonstrate this trend within the upper 0–300 m; mean size (sl) of *C. myersi* decreased with depth. The largest individuals of *A. mitopteryx and P. maculatus* occurred in the 0–70 m layer but they showed no statistical difference in average size with depth.

Discussion

Knowledge of the ichthyonekton species composition in the Weddell Sea is limited because of the lack of data for the whole annual cycle. Hubold (1990) reports a total of 23 ichthyoplankton taxa for the period October to February in the Weddell Sea with a maximum of 16 species occurring during any one month period. In this study, the early stages of more fish species were collected in January–February than had been previously reported for the eastern Weddell Sea. This includes the 18 species (Table 2) collected on the Halley transect and an additional six species (total 24 spp.) at the two less intensively sampled

Table 5. Halley Transect, 0 group *Pleuragramma antarctica*: Size composition (sl mm) and analysis of variance for length frequency in different depth stata

Depth (m)	N	Median	Mean	SD ±	Range	Mean and 95% confidence limits
						------+------+------+------
0–70	505	15	15.3	1.55	10–20	(-*)
70–200	282	16	16.1	1.67	12–21	(-*-)
200–300	252	16	16.1	1.62	12–20	(-*-)
300–500	139	17	17.1	1.55	12–21	(--*--)
500–700	102	18	18.2	1.27	15–22	(--*--)
700–1000	60	17	17.2	1.16	14–20	(---*---)
0–1000	1340	16	16.1	1.78	10–22	(*)
						16.0 17.0 18.0

Oneway ANOVA for 6 depth strata: df = 5 F = 83.6 $P = < 0.0001$ Pooled standard deviation = 1.55

sites in the eastern Weddell Sea (Table 4). The species composition and abundance relations (Table 2) are similar to those reported previously for the Weddell Sea in January–February (Piatkowski 1987; Hubold 1990). This indicates some stability in the seasonal species composition and dominance relations among the ichthyonekton in the south-eastern Weddell Sea during summer.

The 24 ichthyonekton species collected represent only 32% of the demersal species recorded from the region. To date, the early stages of 38 species (51%) of the total of 75 species have been recorded (Table 1). The lack of representation is partly explained by the strong seasonal succession exhibited by Weddell Sea ichthyoplankton (Hubold 1990); a feature that is also characteristic of other regions such as the Antarctic Peninsula (Kellermann 1989) and South Georgia (Burchett et al. 1983; North and White 1987). Another factor is the lack of sampling data from all months of the year from the southern Weddell Sea. The potential period of occurrence of un-represented species can be anticipated with reference to their known reproductive patterns (cf review by Kock and Kellermann 1991). Some closely related species may avoid interspecific competition by temporal or vertical separation. For example, the closely related channichthyids *Pagetopsis maculatus* and *P. macropterus* spawn about six months out of phase and so larvae at similar stages of development do not co-occur. The larval stages of other species undoubtedly will be detected by investigating habitats that are not routinely sampled such as the epibenthic layer close to the seafloor or sympagic habitats associated with the underside of pack-ice. Other species may not be a normal component of the pelagic ichthyonekton. For example, the larval stages of deep-water groups such as the liparids and zoarcids are rarely collected in net samples and are probably demersal.

Hubold (1990) reported the co-occurrence of the early stages of the channichthyid *C. myersi* and the notothenid *P. antarcticum*. These species with the channichthyid *P. maculatus* demonstrated similar distribution patterns along the Halley Transect. The dendrogram of species affinities resulting from cluster analysis of occurrence in samples (Fig. 7) supported this association and also included the notothenid *A. mitopteryx*. A trophic interaction has been implied (Hubold and Ekau 1990) and gut contents analysis of the two channichthyid species confirmed that a major component of their diet was larval fish, mostly *P. antarcticum* (M G White personal observations). Larval *A. mitopteryx* and *P. antarcticum* are specialist copepod predators feeding on the most abundant copepod taxa and stages (Hubold and Ekau 1990). Thus the early stages of these four fish species form a trophic assemblage with the abundant nototheniids preying upon concentrations of small crustaceans and the channichthyids feeding on the most abundant larval fish, the recently hatched and more vulnerable *P. antarcticum*. Competition between *P. antarcticum* and *A. mitopteryx* for copepod prey appears to be minimized by spatial separation through different inshore-offshore and vertical distributions.

Past examinations of Weddell Sea species assemblages have concentrated on distribution patterns parallel to the ice-shelf along the eastern and southern coastal polynya. These studies identified both benthic (Voss 1988) and pelagic (Boysen-Ennen 1987; Piatkowski 1987; 1989) species assemblages associated with different water masses and water column characteristics of the northern and southern shelf areas. The transition between the northern and southern shelf assemblages occurs in the vicinity of Halley Bay. This is associated with the separation of the eastern Weddell Gyre into a southern limb deflected into the Filchner Trench and the westward flowing major component of the East Wind Drift which follows the topography of the continental slope (Fig. 1). The present transect extended offshore within this transition zone and should reflect mixing of the faunal components of the two shelf assemblages. Coast to shelf-edge transects have not previously featured in the studies of the marine ecosystem in the Weddell Sea because of the narrowness of the shelf and the constraints of the semi-permanent ice-fields. The EPOS 3 Halley Bay transect of approximately 245 km traversed the inner-shelf trench and the continental shelf to beyond the shelf-break.

The cluster analyses based on the occurrence of young fish at stations across the shelf indicated three sampling site groupings which were associated with different water mass characteristics and distance from the shore (Fig. 6).

1. A relatively low diversity and low abundance notothenioid group dominated by *A. mitopteryx* occurred in the cold, oligotrophic water of the inner-shelf trench.

2. A more diverse but low abundance notothenioid group occurred over the central continental shelf.

3. A mixed notothenioid/myctophid group of high abundance and moderate diversity occurred over the slope beyond the shelf-break front which was associated with water of the main southern limb of the Weddell Gyre and its extension at the surface over the shelf.

The peripheral ice-shelves of the Weddell Sea apparently have a dramatic effect on the horizontal distribution of the young fish which is different from other known Antarctic areas. At lower latitudes in the Southern Ocean there is commonly a marked transition between a neritic notothenioid assemblage over the shelf to an assemblage dominated by oceanic and mesopelagic species at the edge of the continental shelf. (White and North 1987; Loeb et al. In Press; Koubbi et al. 1992). A neritic to oceanic transition has also been described for the Weddell Sea fish by Hubold (1990) but this differs from lower latitude areas by having a strong notothenioid component in the oceanic assemblage due to large numbers of *P. antarcticum* and the co-occurring channichthyids. This difference may be due to the combination of:

(a) the more pelagic nature of high-Antarctic fish assemblages;

(b) species related differences in larval behaviour and habitat requirements;

(c) hydrographic characteristics and advection processes in the eastern Weddell Sea.

The early stages of *P. antarcticum* are most abundant in the upper 100 m. Prevailing currents advect these southward from spawning grounds in the north-east Weddell Sea. Thick ice-tongues emerging from the ice shelves in the vicinity of Vestkapp and Kapp Norwegia deflect the neritic water-mass and the associated ichthyonekton assemblages offshore over deeper water into the main East Wind Drift. As a consequence, the typical transition between neritic and oceanic pelagic assemblages is confounded by the narrow continental shelf and intrusion of ice-shelves over the continental shelf. Similar conditions occur around the Antarctic Continent and so it is likely that the displacement of neritic species from shallow water habitats is a characteristic feature of the high-Antarctic ichthyofauna. It is also possible that offshore advection of the early life stages may have contributed to the evolution of a more pelagic ichthyofauna.

Examination of the vertical distribution patterns showed that the oceanic paraleparidids, myctophids and bathylagids were largely confined to deeper strata and mostly occurred in the Warm Deep Water. However, some species (*Notolepis coatsi* and the bathydraconid *Racovitzia australis*) which were generally collected at depths >500 m also occurred in the surface layer near the continental shelf-break. Hydrographic observations made during the cruise suggested marked vertical mixing and possible upwelling at the shelf-break front (Rohardt et al. 1990; Fahrbach et al. In Press b). The occurrence of oceanic and mesopelagic species at unusually shallow depths is therefore likely to be the result of vertical displacement at the frontal zone.

A number of Antarctic fish species have extended pelagic periods during their early stages of development. As a consequence, regional current patterns are likely to have had important effects on the evolution of reproductive strategies of the resident species (Loeb et al. In Press). Hubold (1984; 1990) describes the importance of the Weddell Gyre in the life history of *P. antarcticum* and suggests that prevailing surface currents permit larval dispersal southward from spawning grounds on the north-east Weddell Sea shelf to nursery grounds in the south-west. The distribution patterns of young *P. antarcticum* observed during EPOS 3 support his hypothesis. Greatest abundances of *P. antarcticum* and the other dominant species were associated with the strongest horizontal currents. *P. antarcticum* was primarily associated with the core of the western limb of the Weddell Gyre which sweeps along the continental slope and *A. mitopteryx* was associated with the core of the eastern Weddell Sea coastal current.

During EPOS 3 most of the *P. antarcticum* were 'O' group newly hatched larva with mean length 16.1 mm ($n=1340$, SD ± 1.78, range 10–22 mm). The length of *P. antarcticum* at hatching is variously reported as 6–7 mm (Regan 1916) to 8–9 mm (Hubold 1985). The summer growth rate ranges from 0.19–0.25 mm day^{-1} (Keller 1983; Hubold 1985). Consequently the estimated age of the larvae sampled during EPOS 3 (size at hatch 8 mm, median length 15–18 mm) would range from 28–53 days. The mean current velocity in the eastern Weddell Sea is 10–20 cm s^{-1} with maximum rates of up to 68 cm s^{-1} (Fahrbach et al. 1992 b). These advection and growth rates suggest a hatching locality on the continental shelf in the north-earstern Weddell Sea between Atka Bay and Kapp Norwegia, some 48–288 km from the study area.

Most of the ichthyonekton occurred in the upper 70 m layer. The prevalence of young fish in the upper part of the Weddell Sea water column has also been noted by Hubold (1990; 1991) who suggested that these stages occupied levels at which feeding was most favourable. An extended period of calm weather during EPOS 3 resulted in a well stratified water column with a 50–100 m deep upper layer of unusually warm summer water ($+1$°C) which was nearly 3°C warmer than the underlying Antarctic Surface Water (Rohardt et al. 1990). The larval stages of high latitude poikilothermic species have a considerable sensitivity in terms of growth and metabolic rates to small temperature changes (Donal Monahan, Personal Communication 1991). Therefore we believe that, in addition to occurring in favourable feeding conditions, the young fish would gain a significant growth advantage by occupying the warmer strata.

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